## THE ANNIVERSARY ADDRESS OF THE PRESIDENT, Professor Allman, M.D., LL.D., F.R.S.

Recent Researches among some of the more simple Sarcode Organisms.

[Read May 24, 1877.]

(Second Notice.)

In my last year's Address I attempted an exposition of researches among certain lower sarcode organisms to which within the last few years the attention of zoologists had been directed. The subject, however, proved to be so large, and the activity which had prevailed in it so great, that I found it impossible to do justice to it within the limits of a single address. I was therefore compelled to leave untouched much of what was necessary for a complete exposition, and I purpose on the present occasion to take up the subject where I was then obliged to leave it.



Heliophrys variabilis, Greeff (Nuclearia simplex, Cienkowski), under slight compression. a, outer layer; b, pseudopodia; c, nucleus; d, vacuolæ. (After Greeff.)

Cienkowski \* has given the name of Nuclearia simplex to a re-

\* "Beiträge zur Kenntniss der Monaden," Arch. f. mikr. Anat. 1865. LINN. JOURN .- ZOOLOGY, VOL. XIII.

Fig. 1.

markable sarcode organism which lives on the contents of Algacells, which it sucks out in the manner of a *Vampyrella*. It would seem to be identical with the rhizopod to which Greeff gave the name of *Heliophrys variabilis* (figs. 1 & 2)\*, and F. E. Schulze that of *Heterophrys varians*<sup>†</sup>. It has certain obvious relations with the *Heliozoa*, from which, however, it differs in its great variability of form, the spherical or homaxial shape so characteristic of the *Heliozoa* being only occasionally assumed by it.

It is described by Cienkowski as an *Amæba* with fine, pointed, instead of lobose, pseudopodia, and with numerous nuclei in its protoplasm. The protoplasm is very transparent, and besides the nuclei encloses a multitude of vacuoles, which slowly appear and disappear without showing the sudden collapse which is characteristic of the true pulsating vacuoles.

Some of the specimens studied were observed by Cienkowski to have become surrounded by a granular spherical envelope, and to have thus passed into what he regards as probably a resting-stage.

Cienkowski places *Nuclearia*, along with *Vampyrella* &c., in his group of "Monadinæ;" but its structure, and especially the presence of nuclei in its protoplasm, will not justify its association with organisms which are essentially cytodes.

Greeff describes his *Heliophrys variabilis*, which he finds abundant in both stagnant and running water during spring and early summer, as varying from a sphere or circular disk (fig. 1) to an irregular more or less elongated and compressed form (fig. 2). He further describes it as surrounded by a hyaline and homogeneous layer, whose surface is set with short rod-like granules, and which is traversed by the long pointed pseudopodia on their way from the proper body in which they originate to the external water. The numerous nuclei which are brought into view by moderate compression consist of a delicate hyaline capsule with a darker homogeneous central spherule.

A closely allied, if not identical, organism has been described by Hertwig and Lesser under the name of *Leptophrys*. It is a multinucleated greatly vacuolated protoplasm mass of very variable outline, but usually in the form of a delicate veil, which spreads over the stage of the microscope, and is so thin and transparent as to allow objects which lie under it to be distinctly seen. Its edges usually flow out into lobes, from which the fine pointed pseudopodia radiate.

\* Arch. f. mikr. Anat. xi. + "Rhizopodenstudien," Arch. f. mikr. Anat. xi.



Heliophrys variabilis in the act of creeping. It has passed from a globular form to that of an irregular disk. The pseudopodia have become divided. e, rod-like granules of the outer hyaline layer. Other lettering as in preceding fig. 1. (After Greeff.)

Hertwig and Lesser, Eilhard Schulze, and Archer have made us acquainted with a large number of monothalamian Rhizopods of fresh water.

In almost all the freshwater forms the presence of a nucleus can be demonstrated without difficulty; and resting on the belief universally entertained that the marine forms known in general by the name of Foraminifera, whether monothalamian or polythalamian, are, with one or two incompletely established exceptions, destitute of a nucleus, Hertwig and Lesser saw in this difference grounds for the association of the freshwater monothalamic Rhizopods into a special group, to which they limited the name of *Monothalamia*.

The quite recent discovery, however, by Hertwig himself \* and by F. E. Schulze<sup>†</sup>, of a nucleus in several genera of Foraminifera, and the great probability of its occurrence throughout the whole, take away the only important structural difference between the two groups, and render it necessary to embrace both in a single

\* "Bemerkungen zur Organisation und systematischen Stellung der Foraminiferen," Jenaische Zeitschrift, 1876.

† "Ueber den Kern der Foraminiferen," Archiv für mikr. Anat. 1876.

class. To this class Hertwig, in his most recent memoir\*, has assigned the name of *Thalamophora*.

The researches which have thus from various quarters been brought to bear on these organisms have made known to us many new facts, and enable us to give a more complete picture of them than had been hitherto possible.

The *Thalamophora* are organisms whose soft bodies are formed of sarcode or protoplasm which envelopes one or more nuclei, and which for the purposes of locomotion and the prehension of nutriment has the power of emitting pseudopodia. Receptacles of liquid in the form either of contractile or of non-contractile vacuoles are almost always present. All *Thalamophora* are enveloped by a shell or test, which is either purely chitinous or is hardened by calcareous deposits, or incrusted by siliceous fragments. In its shape it belongs to the "monaxial fundamental form" of Haeckel, having a main axis, at one extremity of which is the oral orifice of the test. In the simplest cases this main axis is straight (*Gromia*, *Microgromia, Euglypha, Nodosaria*, &c.), but in most of the marine forms it is regularly curved in a spiral (*Miliola, Rotalia, Polystomella*, &c.), while in some the regular curvature is masked by a subsequent irregularity of growth.

In this monaxial shape and in the constant position of the oral orifice of the test in relation to the main axis we find the essential character by which the *Thalamophora* are distinguished from the *Heliozoa*. These, instead of being monaxial, are "homaxial" (Haeckel); that is, all their axes being of equal value, their proper form is that of the sphere. Further, when a test is present in the Heliozoa, this has either no constant opening, or the openings are numerous and placed without any definite relation to an axis.

By consecutive constrictions of the test at right angles to the main axis polythalamic forms are produced. Carpenter had already shown that the characters derived from the polythalamic or monothalamic condition of the shell are of but slight systematic value; and this view is fully borne out by the most recent researches, which make it evident that the number of the nuclei in the Foraminifera do not stand in any direct relation to the number of the chambers—in other words, that each newly formed chamber does not necessarily contain a newly formed nucleus. The polythalamic forms therefore are not be regarded as colonies of monothalamic forms.

\* Op. cit. Jenaische Zeitschrift, 1876.

A much more important character available for the definition of the higher groups had been shown by Carpenter to be derivable from the structure of the shell. In some this is throughout perforated by minute canals, in others provided only with the single comparatively large terminal orifice, or occasionally with a terminal group of orifices, or in rare cases with two large orifices, one at each end of the main axis. The *Thalamophora* thus admit of a primary division into the *Imperforata* and the *Perforata*, as insisted on by Carpenter.

It may be questioned whether the presence of a test affords a character of sufficient importance to justify its being made the basis of such higher groups; whether, for example, *Arcella* should be far separated from  $Am\alpha ba$  on the grounds that in one case the sarcode is naked, in the other enveloped by a test.

To this character Carpenter assigns a very subordinate value. We must not, however, lose sight of the fact that the formation of a test,—of a true test, at least, as distinguished from a mere pellicle which yields to such changes of form as the sarcode may undergo, -brings with it modifications in some of the most striking characters of the naked protoplasm; for not only are the pseudopodia, even in the Perforata, necessarily limited by it to definite points of the body, but it substitutes a definite outline for the indefinite and constantly changing outline of such naked organisms. The importance of this definiteness of outline is shown by the great symmetry which is in almost every case presented by it, while the shell itself often possesses an elaborate structure, as seen in the hexagonal areolæ between the inner and outer tables of the shell in Arcella and the beautiful tessellated structure in Quadrula and Euglypha.

Hertwig and Lesser have discovered many new freshwater representatives of the *Thalamophora*, and have made known to us many important facts in their structure and life-history. All the freshwater *Thalamophora* hitherto met with are monothalamic (figs. 4, 5, &c.), and, if we except Archer's genus *Diaphoropodon*, are also imperforate. Their test is of a conical or elliptical shape, and is for the most part of a firm and solid consistence, though occasionally membranous and flexible. It is either a pure product of excretion, or in addition to this it may become more or less incorporated with foreign bodies, such as minute fragments of silica or shells of Diatomacea. When it consists of a pure excretion from the protoplasm-body it may be either perfectly smooth and structureless (fig. 4), or it may present various kinds of structure or sculpture, often very elegant and characteristic (figs. 5, 7).

The soft protoplasmic contents of the test are in the freshwater *Thalamophora* almost always differentiated into a more granular portion and a more homogeneous portion. In those with a single orifice the granular protoplasm lies towards the anterior or oral end, the more homogeneous towards the posterior or aboral end. The posterior homogeneous protoplasm includes the nucleus, while in the anterior granular portion, or on the boundary between the two, lie numerous vacuoles. These are almost always rhythmically contractile, and are constant in number and position in each species. When there are two shell-orifices the nucleus lies in the middle point between them. In the *Arcellæ*, which present the condition very exceptional among freshwater *Thalamophora* of being multinucleate, the nuclei lie in the marginal part of the nearly disk-shaped protoplasm.

The characteristic form of the nucleus is that of a clear vesicle, which almost always includes a pale bluish nucleolus.

The pseudopodia present two important modifications. In one (figs. 4 & 5) they are cylindrical, blunt, unbranched, non-confluent, and usually destitute of granule-currents. In the other (fig. 6) they are very contractile delicate pointed threads, which repeatedly ramify and flow together, and present currents of granules in their interior. Between these two, however, there are numerous intermediate conditions, but the two main forms, the blunt and the pointed, may always be distinguished; and Hertwig and Lesser accordingly employ these characters in the definitions of some of their higher groups, adopting from Carpenter the name of *Lobosa*, which they assign to the forms with blunt pseudopodia, and assigning that of *Rhizopoda* to those in which the pseudopodia are pointed.

The name of "Rhizopoda," in the special sense in which it is here employed by Hertwig and Lesser, is certainly objectionable, and from its being very generally used with a different significance would tend to introduce confusion into our definitions. F. E. Schulze uses in the same sense the more appropriate designation of "Filifera;" but Carpenter had long ago employed that of "Reticularia" to indicate those forms whose pseudopodia are long and filiform and tend to unite with one another into a network (*Gromia* and the so-called Foraminifera). As forms occur, however, with filiform pseudopodia which show no tendency to anastomose, the designation "Filifera" is of more general application. Another important systematic character is derived from the number of terminal or oral orifices in the test, though this, in consequence of the great inequality of the two groups based upon it, loses much of the practical value which it would otherwise possess in classification. In almost every case there is but a single such orifice (figs. 4, 5, 6, &c.). In some rare cases, however, there are two, one situated at each end of the main axis (fig. 8). It is these conditions which Hertwig and Lesser designate respectively by the names of *Monostomatous* and *Amphistomatous*.

Among the freshwater *Thalamophora* with blunt pseudopodia (*Lobosa*) Hertwig and Lesser\* have made some interesting observations on the long-known and widely distributed *Arcella vulgaris*, one of the largest and best fitted for observation of the freshwater *Rhizopoda*. They have corrected the descriptions of the structure of its shell given by previous observers, and have brought together its essential characters in a more exact generic diagnosis than had been hitherto attempted.

Its shell, which is a pure excretion from the contained protoplasm, has its main axis very short in proportion to the lateral axes; and the elongate form so characteristic of the freshwater *Thalamophora* becomes thus shield-shaped with the orifice for the pseudopodia in the centre of the flat side, which, during locomotion, is turned towards the supporting surface. Its walls, as now shown by Hertwig and Lesser, are composed of two parallel plates, an outer and an inner, which are united to one another by an intervening structure with hexagonal chambers like those of a honeycomb.

Besides containing contractile vesicles the protoplasm is very exceptional in containing numerous nuclei. The body does not entirely fill the shell, but forms a disk-shaped mass of protoplasm lying on the lower wall and having the contractile vesicles and nuclei immersed in its peripheral parts. It is connected with the upper wall of the shell by filiform processes, which in young specimens are richly developed, repeatedly branch and anastomose, and form a sort of pseudopodial net over which the protoplasmgranules travel to and fro.

An encysting process, apparently connected with reproduction, has been observed by them. In this the protoplasm becomes surrounded by a globular cyst which lies within the shell close to the orifice. The coarsely granular and opaque condition of the protoplasm rendered it impossible for them to discover any thing

\* Arch. f. mikr. Anat. Band x. Suppl.-Heft.

regarding the condition of the nuclei; nor were they able to follow the process through any further stages.

They have also studied a phenomenon which has been regarded by other observers as a conjugation of two individuals, but which Hertwig and Lesser interpret as a case of reproduction by spontaneous division. In this the appearance presented is that of two individuals in union with one another by their pseudopodial surfaces, where they are connected by a broad bridge of protoplasm, which stretches from the soft body of one animal to that of the other. One of these connected individuals has always the usual dark brown shell, while in the other the shell is clear and colourless. Across the connecting bridge the protoplasmic contents of one shell pass over into the other until the former is nearly emptied. Then the direction of the stream is reversed and the nearly emptied shell becomes filled at the expense of the other. This interchange of the contents now repeats itself, and thus goes on rhythmically for some time, when a period of rest sets in, the protoplasm bridge becomes gradually thinner, and finally breaks across, and the two hitherto united Arcellæ become detached from one another, each composed of nearly an equal part of the origiually single protoplasm mass, which, according to the interpretation of Hertwig and Lesser, has thus become divided into two independent segments.

Bütschli has described in Arcella a somewhat different phenomenon, which he regards as a true conjugation\*. In this three individuals, all with dark brown shells, were observed to be in union with each other by means of bridges of protoplasm which proceeded from the shell-orifices. On the day following the separation of the conjugating Arcella he noticed that in one of the individuals the protoplasm-body had withdrawn itself for a considerable space from the shell-wall, and that in the liquid which filled the interval a multitude of Vibrio-like bodies swarmed, while in close contact with the dorsal surface of the protoplasm there lay numerous flat disk-shaped masses of protoplasm. After some time these showed lively amœboid movements, and crept about between the body of the parent animal and the shell-walls. These amœboid bodies ultimately crept out through the shell-orifice. They contained a contractile vacuole and a clear nucleus, and moved by the protrusion of short very blunt processes. Bütschli was not able to follow their further development; but he does not hesi-

\* Arch. f. mikr. Anat. vol. xi. (1875) p. 459, pl. xxv.

tate to regard them as the proper brood of the Arcella, and compares their formation with that of the budding of zoospores from the surface of the body in Noctiluca as described by Cienkowski\*.

We owe to Hertwig and Lesser<sup>†</sup> and to Franz Eil. Schulze<sup>‡</sup> two papers on *Pseudochlamys patella* (fig. 3), in which they supplement and correct the description of this rhizopod as given by Claparède and Lachmann. Its shell is of a brownish-yellow colour, shaped like a watchglass, so as to be widely open on the inferior surface. Here, according to Hertwig and Lesser, a delicate structureless membrane stretches across the opening, which it closes, except in

Fig. 3.

### Pseudochlamys patella.

Viewed from below, with opposite margins of the test folded in, and with a protruded finger-shaped pseudopodium.

(After F. E. Schulze.)



a small central space which remains open for the passage of the pseudopodia. Schulze, who makes no mention of this membrane, describes indications of structure in the shell towards its summit which recalls that of Arcella.

The animal possesses the remarkable power of bringing into juxtaposition the opposite margins of the wide shell-opening, thus completely changing the form of the shell and making it resemble the bivalve shell of a Lamellibranchiate mollusk or of a *Cypris*. This approximation of the margins is evidently brought about by the contractility of the contained protoplasm, while the return to the previous condition would seem to result from the elasticity of the shell. Schulze has noticed in some cases special bands of protoplasm passing from the circumference of the body to the margin of the shell to which they are attached. He believed they act in a way analogous to that of muscles in regulating the form of the orifice.

The protoplasm-body is finely granular, and contains in its periphery a great number of contractile vesicles, while there is a \* Arch. f. mikr. Anat. vol. ix. p. 47. + *Id.* vol. x. Suppl. ‡ *Id.* vol. xi.

single more central nucleus. Besides a single (seldom more) thick finger-shaped pseudopodium like those of *Arcella*, Schulze describes numerous rounded tubercle-like processes, which do not seem to project beyond the orifice.

As in *Arcella*, an encysting process has been observed, but has not been followed to its results.

The authors believe that Greeff has incorrectly assigned to the genus *Amphizonella* the form which he names *Amphizonella flava*, and which they regard as identical with *Pseudochlamys patella*.

The *Pyxidicula operculata* of Ehrenberg is another nearly allied form. Claparède and Lachmann, followed by Carter, had placed this rhizopod in the genus *Arcella*; but Hertwig and Lesser, relying on the fact of the shell being destitute of the characteristic structure of that of *Arcella*, restore Ehrenberg's name.

### Fig. 4.

### Hyalosphenia lata.

Viewed from the broad side, with a slightly divided finger-shaped pseudopodium.

(After F. E. Schulze.)



Hyalosphenia lata, F. E. Schulze (fig. 4)\*, is another freshwater representative of the *Thalamophora*. It has a compressed pyriform test and thick finger-shaped pseudopodia. The test is a simple hyaline case without any trace of structure. Included in the broad aboral portion of the protoplasm is a large spherical nucleus containing numerous nucleoli, and just in front of it lie the pulsating vacuoles, which are usually two in number. There is usually only a single finger-shaped pseudopodium emitted from the orifice of the test. The pseudopodium, though belonging to the lobose type, encloses fine granules, whose flowing movements are easily seen in the axis of the pseudopodium.

\* F. E. Schulze, loc. cit.

Among the *Thalamophora* with thick, blunt, non-anastomosing pseudopodia, must also be included a beautiful freshwater rhizopod originally described by Wallich\* under the name of *Difflugia* symmetrica, and more recently studied by Fr. Eil. Schulze, who has made it the type of an independent genus to which he assigns the name of *Quadrula* (fig. 5)<sup>†</sup>.

The test is pear-shaped, laterally compressed so as to be elliptical in transverse section, and presents a definite sculpture caused by its being composed of a great number of hyaline square plates which touch one another by their edges. *Quadrula* is nearly allied to *Hyalosphenia*, from which it differs mainly in possessing a definitely sculptured test. The granular pro-



Fig. 5.

Quadrula symmetrica. Viewed from the broad side. (After F. E. Schulze.)

toplasm-body does not in general completely fill the test; and the space which intervenes between it and the test-walls is occupied by a clear liquid and traversed by thin bands of protoplasm.

In the centre of the more voluminous posterior or aboral portion of the body lies the large clear spherical nucleus with a very distinct dark nucleolus; and in front of this are the pulsating vacuoles, generally two in number. The pseudopodia are few, and are

\* Ann. Nat. Hist. vol. viii. 1864. † Arch. f. mikr. Anat. vol. xi. 1875.

thick and finger-shaped and, like those of *Hyalosphenia*, enclose fine granules.

In the fact of its shell being composed of numerous juxtaposed plates *Quadrula* presents an obvious affinity with *Euglypha*, from which, however, its compressed form and, above all, its thick fingershaped pseudopodia clearly separate it. In tests from which the protoplasm has disappeared detached plates similar to those composing the walls are frequently found either lying free or associated in bundles. A fact of quite a similar kind has been noticed in *Euglypha*.

Hertwig and Lesser have studied the Difflugia and have described a new species (*D. acropodia*) remarkable for the peculiar form of its pseudopodia, while they bring together the essential characters of the genus more exactly than had been hitherto done. The genus *Difflugia* was founded by Leclerc for freshwater *Thalamophora* with blunt pseudopodia, and whose test provided with a single opening is not a pure excretion of the protoplasm, but is formed of agglutinated foreign corpuscles—fragments of silica and shells of Diatomacea. The shell so constructed, however, has, as the new species examined by Hertwig and Lesser clearly shows, a membranous basis excreted by the contained protoplasm.

The *Difflugiæ* have a nucleus immersed in the posterior part of the protoplasm; but no contractile vesicles have as yet been discovered. Like the Heliozoa they contain also in their protoplasm chlorophyl-granules, a fact of extremely rare occurrence among the *Thalamophora*.

In *D. acropodia* the pseudopodia differ from the finger-shaped processes of other *Difflugiæ* in consisting of broad plates of homogeneous protoplasm, which at some distance from the pseudopodial opening end in irregularly-shaped lobes with their contours cut into sharp segments. They owe their origin to the confluence of what were at first narrow lancet-shaped pseudopodia very like those of *Actinosphærium*, except in being destitute of granules. They form an obvious transition between the blunt pseudopodia of the *Lobosa*, and the pointed pseudopodia of those forms to which Hertwig and Lesser would confine the name of *Rhizopoda*, the *Filifera* of F. E. Schulze.

The siliceous fragments with which the test is set are usually so sparingly scattered  $\mathbf{a}$ s to reveal the thin basal membrane on which they are fixed.

The Thalamophora with pointed filiform pseudopodia (Filifera)

are much richer in genera and species than the *Lobosa*; and we have here, as in the *Lobosa*, forms in which the shell is a pure excretion from the protoplasm, and others in which it is strengthened by the incorporation of foreign bodies. The first group may be further subdivided into those whose shell is structureless, and those in which it is characterized by the possession of definite sculpture.

To those in which the test is a simple structureless excretion without the agglutination of foreign particles must be referred the genus *Gromia*, founded by Dujardin.

Its more or less spherical or oval test lies close upon the surface of the protoplasm-body; it is membranous, flexible, and inelastic, and through an opening at one end of its main axis the pseudopodia are emitted and form by their repeated branching and anastomoses a widely extended protoplasm-network. No contractile vacuoles have yet been found.

Gromia oviformis, on which Dujardin founded his genus, is a marine form. It has been made the subject of a careful study by Max Schultze, who, instead of the single nucleus which almost universally characterizes the freshwater *Thalamophora*, has found in the posterior part of its body numerous clear spherical vesicles filled with granules and regarded by him as nuclei.

A new species of Gromia, G. granulata, F. E. Schulze, has been studied by F. E. Schulze, who found it in fresh water attached to Ceratophyllum and other water-plants. It is a transparent and colourless species, with its clear protoplasm containing a multitude of strongly refringent granules, which at the periphery are disposed at nearly equal intervals, so that when seen through the transparent shell they give to this the appearance of being minutely punctate. Schulze describes a single nucleus lying in the posterior part of the protoplasm. It is a large, clear, spherical body, surrounded by a membrane, and having within it either a moderately large, spherical, strongly refringent nucleolus, or many less distinct dark corpuscles. This is pretty nearly the normal condition of the nucleus in the freshwater Thalamophora, and is so very different from the numerous vesicle-like bodies described by Max Schultze as nuclei in Gromia oviformis as to lead us to doubt the correctness of attributing to these last the significance of true nuclei.

The genus *Trinema*, founded by Dujardin for a freshwater Thalamophorous Rhizopod, to which he gave the name of *T. acinus*, and which, under that of *Difflugia enchelys*, was subsequently described by Ehrenberg, has been recently studied by Hertwig and Lesser. It is provided with a firm structureless shell which does not closely invest the protoplasm. It has an elongate oval form, becoming wider towards the aboral pole. The shell-orifice instead of lying at the end of the main axis, lies laterally and oblique to it, and has its margins inflected inwards. The protoplasm-body consists of a posterior homogeneous portion and an anterior more granular portion. In the posterior is the nucleus with its nucleolus, and on the boundary between the posterior and middle third, lying in an equatorial plane, are the contractile vacuoles, which are always three in number. The filiform and pointed pseudopodia are destitute of granules and form no anastomoses.

Hertwig and Lesser describe a peculiar mode of cyst-formation in *Trinema*. They have frequently found specimens of *T. acinus* which contained in the posterior part of the shell a spherical cystlike body filled with uniform strongly refringent granules. A nucleus with nucleolus were also generally visible in it. In some cases the cyst was seen to be invested by a double membrane, apparently analogous to the double investment observed by Hertwig and Lesser in the cysts of *Euglypha alveolata* (see the description of this rhizopod given below).

They have also found examples of *Trinema* in which the posterior part of the shell was no longer occupied by the protoplasmbody, which had the appearance of being truncated posteriorly. In one of these the otherwise empty space was nearly filled by a constantly rotating sphere. Whether the rotation was caused by cilia or flagella, they could not ascertain; but they believe that here, as in *Microgromia*, the detached body was formed by a self-division of the protoplasm, and is destined to become liberated as a swarm-spore.

Like many other freshwater Thalamophora, two individuals of *Trinema acinus* are often found united to one another by their pseudopodial orifices. No change has been noticed as the result of this union, which has probably nothing to do with reproduction.

Claparède and Lachmann consider the Euglypha pleurostoma of Carter as identical with Dujardin's Trinema acinus; and this view is accepted by F. E. Schulze, who attributes to Trinema a sculptured shell like that of Euglypha. With this identification Hertwig and Lesser do not agree. They believe that Carter has rightly referred his rhizopod to the Euglypha.

To the same group of freshwater filiferous Thalamophora belong the species referable to Claparède and Lachmann's genus Plagio-Hertwig and Lesser correct and supplement the descripphrys. tion of this genus given by Claparède and Lachmann, who, regarding it as destitute of shell, place it in their family of the Actinophryidæ. It is really provided with a delicate membranous flexible test, which is thrown into folds by the various movements of the body. According to Hertwig and Lesser's amended description, the Plagiophryses are monothalamic Thalamophora with definite and but slightly varying body-forms and with branched filiform pseudopodia which seldom or never anastomose. They have a delicate test, which lies close upon the body, participates in the slight changes of shape of the included protoplasm by becoming thrown into folds, and is provided with a single orifice for the passage of the pseudopodia. Two new species are described.

Hertwig and Lesser\* have raised the Arcella hyalina of Ehrenberg into a new genus under the name of Lecythium. This rhizopod has been further examined by Cienkowski †.

Its nearly spherical membranous shell is of a crystal clearness, and is closely applied to the protoplasm. The pseudopodial orifice, which is borne by a very short neck, is situated a little to one side, so that the shell possesses a slightly bilateral symmetry. The protoplasm presents a posterior almost perfectly homogeneous division in which is imbedded the large spherical nucleus with its nucleolus, and an anterior granular division rich in vacuoles, which show no pulsation. It is especially distinguished by its greatly developed pseudopodia-emitting mass of protoplasm (*Pseudopodienplatte*) which pours itself out of the shell-orifice in order to send forth strong radiating and rarely anastomosing pseudopodia, and which either forms an amorphous mass or envelopes the entire body with a pseudopodial mantle.

*Lecythium* usually forms colonies in grape-like clusters with a common pseudopodial plate; the colonies result from a longitudinal division of the rhizopod.

Nearly allied to *Lecythium* is a monothalamic rhizopod to which Cienkowski gives the name *Chlamydophrys stercorea*, and which he frequently met with during his researches among fungi

\* "Ueber Rhizopoden," &c. Arch. f. mikr. Anat. Band x. Supplement-Heft. † "Ueber einige Rhizopoden und verwandte Organismen," Arch. f. mikr. Anat. 1875. which inhabit the excreta of animals. He regards it as identical with the Difflugia enchelys of Schneider. It has a clear glassy shell destitute of sculpture.

Its reproduction takes place by the protrusion from the shellorifice of a mass of protoplasm in which a nucleus makes its appearance independently of that of the parent. The protruded protoplasm soon becomes invested by a delicate shell, and the whole might now be easily mistaken for two individuals in conjugation. At the same time pseudopodia radiate from the common bridge of protoplasm, and finally the two parts separate from one another.

But Chlamydophrys is, like Lecythium, a colony-forming rhizopod; and in this case the zooids formed by successive constrictions of the protruded protoplasm remain united to one another so as to form the grape-like clusters with the shell-openings directed towards the common point of union originally observed by Schneider.

Cienkowski frequently found individuals with two, three, or A similar multinucleate condition occurs in Armore nuclei. cella, Actinosphæria, and Nuclearia. The real significance of this character, which has an obvious bearing on the unicellular theory of the Protozoa, is not very evident. It is possibly, as suggested by Cienkowski, the beginning of a zoospore-formation or of fission.

To the development-cycle of Chlamydophrys belongs also a resting-state which, as in other cases, appears to be conditioned by the drying up of the locality. When passing into the resting-state, the entire body escapes from the shell, assumes a spherical shape, and clothes itself with a thick membrane. In the grape-like clusters the resting-state is introduced by all the members of the colony with their common protoplasmic basis becoming fused together and enveloped in a single cyst.

In the same group of single-chambered Thalamophora is an elegant little rhizopod to which Archer, who first described it, gives the name of Gromia socialis, and which possesses, like Lecythium and Chlamydophrys, the curious habit of becoming united with neighbouring individuals into a common colony by the mutual fusion of the pseudopodia.

Archer's G. socialis has been further investigated by Hertwig, who has raised it into a new genus under the name of Microgromia\*.

In a highly interesting and important memoir he has given us \* "Ueber Microgromia," Schultze's Archiv, Band x. Supplement-Heft.

the results of a careful study of this remarkable little rhizopod (fig. 6). The nearly globular shell is prolonged into a short neck, which carries the pseudopodial orifice. It thus allows an oral and aboral pole to be distinguished, while the orifice being a little to one side gives to the shell a slightly bilateral symmetry.

Fig. 6.



### Microgromia socialis.

A, a colony in its extended state; some of the individuals seen in longitudinal fission. B, a colony in its compact or cystophrys state; some of the individuals at a distance from the main heap. C, formation of a swarm-spore; the portion which is to become a swarm-spore has advanced towards the anterior end of the shell. D, further stage in the formation of a swarm-spore; the portion which is to become a swarm-spore escaping through the orifice of the shell. E, one of the swarm-spores now complete and free. (After Hertwig.)

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The protoplasm passes outwards through the neck, and expands fungus-like over the margin, where it attaches the body to the shell. From this fungus-like expansion the pseudopodia radiate in all directions.

The body consists of a pale bluish protoplasm with its anterior half granular and its posterior half almost perfectly homogeneous. In the posterior is imbedded the nucleus. This possesses the form common to the nuclei of almost all the freshwater Rhizopoda —that of a clear, perfectly colourless, spherical body containing concentrically within it a spherical pale-bluish nucleolus. The membranous investment which, in some Rhizopods, surrounds the nucleus is here wanting. In the anterior granular portion of the protoplasm lies the contractile vacuole.

Hertwig and Lesser find the individuals not only united by their pseudopodia into the loose colonies described by Archer (fig. 6, A), but also, by a close union, constituting botrylliform clusters (B). He regards these botrylliform clusters as identical with a form described by Archer as an independent organism under the name of *Cystophrys Haeckeliana*, which is thus, according to Hertwig, nothing more than a heap of *Microgromia socialis*.

Hertwig has further found that M. socialis multiplies itself by means of locomotive germs, a discovery of importance in its bearing on the development-history of the Monothalamia. He has seen the protoplasm of the various members of the colony divide by a transverse constriction into two halves. each with its nucleus and its contractile vacuole. The posterior segment remains for some time free in the bottom of the shell and then presses forward (C), and, by means of amœboid movements, escapes through the pseudopodial orifice (D). After its escape from the shell the amœboid movements continue, and the germ now stretches itself out into the form of a worm, or contracts into a globe, or forms a lobed mass of protoplasm spreading over the pseudopodia of the mother colony. It then gathers itself together, acquires an oval form, develops from one end a pair of flagella, and forsakes the colony as a free-swimming swarmspore (E); or, in other cases, instead of becoming a flagellate swarm-spore, assumes an Actinophrys-like form and moves about by the aid of three or four more or less branched pointed pseudopodia. Hertwig was not able to trace them to their ultimate destiny; but there can be little doubt that both kinds of locomotive germs come, after a time, to rest, excrete a shell, and lay the foundations of new colonies.

The observations of Hertwig render it probable that the simple extension of the colony without separation of the newly formed zooids takes place by a longitudinal instead of a transverse division of the body. Two or, in some cases, three segments are thus formed. Of these, one remains in the old shell, the others forsake it and excrete for themselves a new one, while all continue in union by their common pseudopodial end.

Cienkowski\* has, in all important points, confirmed these observations. He finds further that the second cell-nucleus which appears during the division of the shell-contents arises independently, and not by the division of the mother nucleus.

Among the genera of Thalamophora in which the shell possesses a definite structure, Euglypha (fig. 7) may be regarded as the most typical. This genus was founded by Dujardin, and Hertwig and Lesser retain in its essential points the definition given by the French observer. The Euglypha are Rhizopoda with pointed filiform pseudopodia which show no granule-currents, and do not anastomose with one another, but for the most part ramify dichotomously. The oval or flask-shaped shell is a pure secretion from the surface of the protoplasm, and remains unchanged under the action of concentrated mineral acids and of alkalies. The terminal orifice is, for the most part, finely dentate, and the solid and inflexible walls of the shell have a sculpture which, as was first pointed out by Carter and by Wallich, is caused by spirally disposed plates which, in all the forms examined by Hertwig and Lesser, are hexagonal and in contact by their edges.

In the protoplasm may be distinguished an anterior and a posterior region. The former occupies nearly two thirds of the whole. The protoplasm of the anterior region is finely granular; it alone contains the foreign matter ingested for nutriment. The protoplasm of the posterior third is homogeneous, but frequently contains some darkly coloured granules of nearly uniform size. In all cases it contains the cell-nucleus first observed by Carter. This has the form so well known in the nucleus of the Rhizopoda, that of a roundish or oval vesicle with a central homogeneous pale blue oval nucleolus. Included in the protoplasm, at the boundary between the anterior and posterior regions, are the contractile vacuoles, generally two or three in number.

F. E. Schulze has studied these vacuoles in Euglypha alveolata,

\* "Ueber einige Rhizopoden und verwandte Organismen," Arch. für mikr. Anat. 1875. Dujardin (fig. 7), one of the finest of the freshwater Monothalamia, and has determined the time which intervenes between each systole. He has found that, at a temperature of 16° Réaumur, this was almost exactly 90 seconds. The pulsation was of that kind which is general among the Rhizopoda, a rapid contraction followed by a gradual accumulation of a clear liquid in the same place until the vacuole becomes once more completely filled, then another sudden collapse, and so on.

Hertwig and Lesser have made some further interesting observations on *Euglypha alveolata*. They have observed in it the structures which Carter calls "granuliferous cells," and which he believes to be produced by the division of the nucleolus, and to be connected with the formation of spermatozoids. Hertwig and Lesser, however, have been unable to assert any thing regarding the economy of these "granuliferous cells." They are roundish vesicle-like bodies irregularly scattered through the protoplasm outside of the nucleus, and more or less filled with small round bluish granules, which mostly appear arranged in regular concentric circles. They show a great resistance to concentrated acetic acid, a fact which is scarcely consistent with their derivation from the nucleolus; and when present they are usually in considerable number, without either the nucleus or the nucleolus having disappeared.

*Euglypha alveolata* is remarkable for the rich development of its pseudopodia, and for the frequency of their subdivision. They mostly spring from broad-lobed homogeneous processes of the protoplasm.

Within the shell of *Euglopha alveolata* may often be seen detached plates resembling in size and form those of the shell itself. They have been noticed by different observers, but more especially by Hertwig and Lesser and by F. E. Schulze. In individuals in which the living protoplasm is still included, they lie upon its surface in a layer parallel to the shell-walls. They are probably destined for the building up of a new shell after the shedding of the old one, or, as Hertwig and Lesser suggest, may be connected with the formation of the inner shell in the peculiar encysting process which they have studied in this rhizopod. Similar plates have also been found by Hertwig and Lesser in the *E. ampulacea*, Dujardin.

The encysting process (fig. 7) which Hertwig and Lesser have studied in *E. alveolata*, and which had been previously noticed by Carter, is very remarkable. Its peculiarity consists in the fact that the cyst is not immediately surrounded by the outer shell of the rhizopod, but by a second shell which lies within this and is



Fig. 7.

### Euglypha alveolata.

Encystation with the formation of a double cyst-covering.

a, the colourless shell formed of hexagonal plates and closed at d by agglutinated foreign bodies; b, the outer brown egg-shaped cyst-shell; c, the inner spherical colourless cyst-shell; f, the homogeneous colourless cord which extends through the space between the inner and outer cyst-shell; n, the clear inner portion of the contents of the cyst, apparently corresponding to a nucleus. (After Hertwig and Lesser.)

completely closed. This inner shell is oviform, with the narrow end turned towards the pseudopodial orifice of the outer shell, within which it lies free and movable. Its structure resembles that of the outer shell; but it is of a light brown colour, which is intensified by the application of sulphuric acid and iodine, while these reagents cause no change in the colour of the outer shell.

Within the inner shell lies the proper cyst. This is of a

spherical form; and in all the specimens examined its contents consist of minute granules which by their strong refringency render the whole dark and opaque, and make an exact knowledge of the contents of the cyst impossible, though a lighter central portion, probably a nucleus, can be distinguished from a darker cortical portion. The cyst consists of a nitrogenous membrane, and has a finely punctured structure; it is connected with the narrow end of its closed investing shell by a thin solid homogeneous cord. The formation of the cyst and its investing shell is accompanied by the closure of the outer shell-orifice by a temporary plug formed by foreign bodies, such as filaments of Algæ and shells of Diatoms.

Hertwig and Lesser regard all this as nothing more than an example of the encysting process so widely distributed among the Rhizopoda, and whose original object consisted most probably in protection against the evil consequences of the drying up of the surrounding water, but which in many cases has become further subservient to a multiplication by self-division of the protoplasm.

The genus Cyphoderia was founded by Schumberger for a beautiful little monothalamian rhizopod which he obtained from fresh water in the Vosges and in the Jura, and described under the name of C. margaritacea. This is the same rhizopod which Max Schultze found in the Baltic, and to which he assigned the name of Lagynis baltica. It has been most recently studied by Hertwig and Lesser and by F. E. Schulze. It is remarkable for the elegant form of its shell, which, instead of being oval, as in Euglypha, has its anterior end produced into a short curved neck so as to give to the shell somewhat the form of a retort. The shellstructure resembles that of Euglypha except in the smallness of its component plates and the absence of distinct serration at the orifice. The contractile vacuoles are in the anterior region of the protoplasm, instead of lying, as in Euglypha, on an equatorial plane between the anterior and posterior.

F. E. Schulze has obtained this rhizopod from very different localities, and from both fresh, salt, and brackish water. He finds the posterior part of the shell often containing only water, through which bands of protoplasm pass from the soft body to the shell-walls. In the midst of the thick posterior part of the body is always a large, clear, spherical nucleus in which one or more dark roundish nucleoli can be demonstrated. The pseudopodia are destitute of granules, divide at acute angles, run out into fine points, and seldom anastomose. He describes a narrow membranous margin surrounding the orifice and overlooked by other observers.

Among specimens obtained from the Baltic, Schulze has occasionally met with two individuals united to one another by the pseudopodial extremities; but he has not followed this phenomenon further.

Under the name of *Cyphoderia truncata* Schulze has described a species in which the main axis is not curved, and has the shellorifice transverse to it; but it is difficult to see how such a form can be referred to the genus *Cyphoderia*.

The genus *Pleurophrys* was founded by Claparède and Lachmann for a freshwater monothalamian rhizopod which resembles *Difflugia* in the fact of its test being composed of foreign particles united by a cement excreted from the surface, while it differs from this genus in its pseudopodia being filiform and pointed instead of being finger-shaped and blunt. The *P. sphærica*, Clap. & Lach., has been further studied by Archer and by Hertwig and Lesser and F. E. Schulze, all of whom have described new species. It appears to be an abundant form, though it has been rarely noticed, a fact which Archer explains by calling attention to the peculiar appearance of its test, which resembles the excreta of Rotifers and other microscopic animals, and which would thus easily cause it to be overlooked. The foreign particles incorporated in its test resist the action of concentrated acids, and are probably siliceous.

The pseudopodia issue from a rather large roundish orifice situated on one end of the longer axis. They are hyaline, very fine, and pointed, divide frequently at acute angles, and anastomose with one another. Hertwig and Lesser differ from Archer in describing them as enclosing granules. Archer has demonstrated the presence of a nucleus.

Archer has noticed in *Pleurophrys amphitrematoides*, Arch., the presence of chlorophyl granules, a fact also observed in *Difflugia*, but not elsewhere met with among the freshwater Thalamophora. In examples of *P. amphitrematoides*, however, examined by F. E. Schulze, this observer has found the chlorophyl granules replaced by round colourless refringent granules quite like them except in the absence of colour.

Hertwig and Lesser have frequently met with two individuals in apposition by their pseudopodial openings, and with the pseudopodia of one confluent with those of the other. Archer has noticed a similar conjugation in another species, with streams of the granular protoplasm passing to and fro from one into the other.

Diaphoropodon mobile, Archer, which is one of the largest of the encased freshwater Rhizopoda, has a rude test formed of heterogeneous foreign particles loosely aggregated round its elliptical body. From an aperture in one end of the test the sarcode mass protrudes in the form of a hemispherical projection, and from this are emitted numerous hyaline branching pseudopodia, which frequently attain an enormous length. But the most singular character of the genus is found in the fact that from the whole of the included surface of the sarcode body are emitted very numerous, short, simple, hyaline pseudopodia which traverse the outer case, giving to its surface the appearance of a dense flocculent clothing. The animal is further remarkable in the possession of a marginal pulsatile vesicle like that of Actinophrys. A large globular nucleus is immersed in the body.

In none of the Monothalamia now described have more than one definite orifice been detected. In *Diaphoropodon* alone, besides the definite single orifice, there would appear to exist in the membranous basis of the test a vast multitude of minute pores through which delicate pseudopodial filaments are emitted, and which call to mind the condition of the true Perforata. All these constitute the *Monothalamia monostomata* of Hertwig and Lesser. There exist, however, forms in which two definite pseudopodial orifices are present; these are the *M. amphistomata* of the same authors.

One of these has been recorded by Barker \* under the name of *Diplophrys Archeri* (fig. 8), and has more recently been made the subject of some very interesting observations by Hertwig and Lesser†. It has a simple elliptical membranous test and, notwithstanding its minuteness, is rendered conspicuous by a bright yellow fat-globule enclosed in its sarcode. The two orifices from which the brushes of pseudopodia radiate are nearly, but not exactly, at opposite ends of the longer diameter of its oval test. Each brush springs from the extremity of a short stem-like process of the sarcode. The conspicuous large yellow globule in the interior consists apparently of a solid fatty matter. Near to this is a nucleus

\* Quart. Journ. Micr. Sci. vol. xvi.

† "Ueber Rhizopoden " &c., Arch. f. mikr. Anat. vol. x.



Diplophrys Archeri.

A, lateral view: a, brilliant yellow fatty body; c, c, c, contractile vacuoles; n, nucleus; c, c, the two opposite pseudopodial orifices. B, a group composed of four segments showing the mode in which the so-called cystophrys-heaps are formed. (After Hertwig and Lesser.)

with its nucleolus, while several contractile vacuoles are distributed through the sarcode.

The observations of Hertwig and Lesser have led them to the conclusion that the *Diplophrys* is multiplied by a process of continuous binary fission, the resulting brood remaining for some time united to one another in little heaps (fig. 8, B). They think that the individuals which thus become divided are destitute of shells. They have further convinced themselves that what Archer describes as an independent organism under the name of "Cystophrys oculea" is nothing more than one of these heaps of young *Diplophrys*, whilst they also show that Greeff was equally in error when he supposed that the *Diplophrys* was a development stage of the heliozoan *Acanthocystis spinifera*.

On fresh horsedung kept under a bell-glass in summer Cienkowski has seen minute yellow globules of the size and appearance of a mucor sporangium. When these little globules are touched under the microscope, they may be seen to break up into a multitude of oval or lenticular corpuscles, which scatter themselves over the field. These are cells containing a nucleus, one or two contractile vesicles, and a yellow pigment-globule. We may perceive in them a slight jerking motion, while on each end one or two long pseudopodia have become apparent. After a time the cells become united to one another in chains by their pseudopodia, or are aggregated in heaps. The chains of cells remind us strongly of the *Labyrinthulea*. They move about, creep over the surfaces, and finally unite into the little yellow globules in which they were first noticed.

Cienkowski places this curious little organism in the genus *Diplophrys*; though, from its minuteness, it is not easy to say whether it is naked or furnished with a shell. He assigns to it the specific name of *stercorea*.

The only form of multiplication observed in it is by fission, as in *Diplophrys Archeri*. During the fission the yellow pigmentglobule in its interior participates in the division.

Another amphistomatous freshwater rhizopod nearly allied to *Diplophrys*, from which it differs mainly in its elliptical test being strengthened by the incorporation of foreign particles, is Archer's genus *Amphitrema*<sup>\*</sup>. At each end of the longer diameter of the test is a round orifice through which is emitted a dense tuft of branching pseudopodia.

Among the most important results derived from recent study of the Rhizopoda is the discovery of a nucleus in the so-called Foraminifera. The failure of all previous attempts to demonstrate the presence of a nucleus in the calcareous-shelled marine Rhizopoda, whether monothalamian or polythalamian, led to the belief that they possessed the morphological value of a cytode or non-nucleated protoplasm mass, and they were accordingly relegated to the lowest stage in the systematic arrangement of the Rhizopoda.

This view must now be abandoned; for the independent and nearly simultaneous researches of Hertwig<sup>+</sup> and of Franz Eilhard Schulze<sup>‡</sup> have demonstrated the presence of a nucleus in representatives of all the principal divisions of the Foraminifera, and justify us in the general conclusion that their protoplasm is in every case nucleated.

By the aid of dilute chromic acid and subsequent tinging with carmine, Hertwig succeeded in demonstrating a nucleus in young specimens of *Miliola*, which as yet consisted of but a single chamber, as well as in older ones where additional chambers had been formed. In the latter case the number of the nuclei was

- \* Archer, loc. cit.
- † Jenaische Zeitsch. vol. x. (1876).
- ‡ Arch. f. mikr. Anat. vol. xiii. (1876).

also generally increased, but not necessarily in the same ratio as that of the chambers. In some of the chambers there occurred only one nucleus, while others contained several.

The nucleus appears to enclose a nucleolus and to be invested by a membrane, thus corresponding in its structure with that of the freshwater Monothalamian Rhizopods.

Similar results followed the employment of the same method of investigation in *Rotalia* and in *Textillaria*, in both of which genera Hertwig succeeded in demonstrating the presence of nuclei.

Schulze had already seen what he regarded as a nucleus with nucleolus in one of the Foraminifera, *Quinqueloculina fusca*, Brady\*; and he now finds an undoubted nucleus lying near the posterior end of the shell in *Entosolenia globosa*, one of the marine monothalamian rhizopods belonging to the family of the Lagenidæ.

In the very abundant polythalamian rhizopod *Polystomella* striatopunctata he has also demonstrated the presence of a nucleus, and has carefully followed out its relations.

The nucleus here has a manifest thick outer membrane with clear contents in which were several strongly refringent roundish bodies. Usually only one such nucleus was to be found in each *Polystomella*, and then always near the middle of the series of chambers; but occasionally two or three occurred each in a separate chamber.

From the dependence of the position of the nucleus on the entire number of the chambers, it is obvious that it must be continually migrating from one chamber to another through the canals of communication. Indeed the nucleus may frequently be seen still engaged in one of the canals between two neighbouring chambers, so as to be partly in one and partly in the other.

From the fact of the many-chambered *Polystomella* containing, as a rule, only one nucleus, we should be justified in assigning to it the morphological value of a single cell; and even in those cases in which in this and other Foraminifera several nuclei have been seen, this multinucleate condition cannot be regarded as indicating a multicellular structure of the organism. It is probably connected with reproduction; and an observation of Hertwig on *Rotalia* contributes some additional facts to our knowledge of the reproduction of the Foraminifera, hitherto observed in but very few instances.

\* Arch. f. mikr. Anat. vol. xi.

Hertwig noticed on the walls of the jars containing living specimens of *Rotalia* little heaps of from twenty to forty small 3chambered individuals which were united to one another by their protoplasm, and in each of which he succeeded in demonstrating a single nucleus. Max Schultze had shown that in some other genera the young are not only developed within the shell of the maternal animal, but become invested with their own shell before leaving the parent; and it is highly probable that these little colonies of young *Rotalia* have a similar origin.

From what is thus known of the reproduction of the Foraminifera, we may conclude that the protoplasmic body of the parent breaks up into segments, conditioned by the nuclei which had been developed in it, while each of these segments forms for itself within the maternal shell its own investment. In *Rotalia* they would seem to become free by the destruction of the parent shell and then to live for a time in union with one another.

The discovery of a nucleus in the Foraminifera will now determine the place which we must assign to them among sarcode organisms; and F. E. Schulze has accordingly attempted by means of a hypothetical genealogical tree to express the descent and mutual affinity of all the leading groups of the Rhizopoda. He employs this designation in a wider sense than has been accepted by many recent zoologists, and embraces under it all those low organisms which, during the greater part of their lives, and especially during the period of their highest development, are brought into relation with the external world by means of pseudopodia, which they employ for locomotion and for the prehension of nutriment. All these organisms agree essentially with one another and constitute a definite group, whether a nucleus be differentiated or not, whether pulsatile vacuoles or hard parts be present or absent, or whether the pseudopodia present the condition of broad lobes, of fine filaments, of a complex network, or of any other modification.

The base of the tree where its stem is as yet undivided consists of the primitive forms—mere non-nucleated cytodes—represented by Haeckel's Monera (Protamæba, Protogenes, Protomyxa, Myxodictium, &c.). From these, by the differentiation of a nucleus in their protoplasm, are evolved the nucleated forms (Amæba, freshwater Monothalamia, Foraminifera, Heliozoa, &c.) which constitute the subdivisions into which the stem branches off. These repeat the various modifications of pseudopodia (lobose, filiform, &c.) which had already existed in the earlier forms, and which they thus derive by inheritance from their non-nucleated progenitors. Finally, through the branch of the *Heliozoa* we are conducted to the ultimate twigs formed by the families of the *Radiolaria*, in which we find not only nuclei, but a "central capsule," indicating the highest grade of differentiation attained by any members of the group.

In 1863 Cienkowski published the results of a series of careful observations on the development of the  $Myxomycetx^*$ , a group of very low organisms which had been unhesitatingly assigned to the fungi, until De Bary had a few years previously called attention to their real nature, and in a very important memoir  $\dagger$  pointed out the predominance in them of characters which had been generally regarded as the proper attribute of animals. De Bary believed that the facts which he had demonstrated in the structure and life-history of the Myxomycetx would render necessary their removal from the vegetable and their relegation to the animal kingdom.

Shortly after the appearance of De Bary's memoir, some further important observations on the Myxomycetx had been made by Currey<sup>‡</sup>, who fully confirmed the production by them of free locomotive bodies resembling the zoospores of an Alga.

The researches of De Bary, of Currey, and of Cienkowski have now made us well acquainted with the structure and development of these extraordinary organisms. A typical Myxomycete (fig. 9) consists of a network of ramifying and anastomosing threads of a slimy or creamy consistence, which spreads over the surface of decayed leaves and stems  $(\Lambda)$ .

From various parts of this slimy network there arise oval vesicles (sporangia) (B) with membranous walls, within which the reproductive bodies or spores are developed.

De Bary was the first to show that the basal network is composed of a substance possessing all the characters of animal sarcode, and his observations have been fully confirmed and further extended by subsequent observers, more especially by Cienkowski. Under the microscope the threads composing the network exhibit active spontaneous movements, which in the larger branches are visible under an ordinary lens or even by the naked eye. A

<sup>\* &</sup>quot;Zur Entwickelungsgeschichte der Myxomyceten," Prings. Jahrb. 1863.

<sup>† &</sup>quot;Die Mycetozoen," Zeitschr. f. w. Zool. 1860, vol. x.

<sup>‡</sup> Natural History Review, No. viii., Oct. 1862.

succession of undulations may be then noticed passing along the course of the threads; and under higher magnifying-powers the characteristic sarcode currents show themselves in constant streams of granules flowing along the threads and streaming from branch to branch of this wonderful network. Here and there

Fig. 9.

## 

Development of the Myxomycetæ.

A, the plasmodium of *Didymium serpula* (natural size). B, sporosacs of *Arcyria flava*: a, young sporosac;  $a^*$ , sporosac in the act of bursting; b, capillitium exposed after the bursting of the sporosac and the diffusion of the spores. C, ripe spore of *Physarum album*. D, the same, with its contents escaping. E, the contents become free, and showing nucleus and contractile vacuoles. F, the same, after having developed a flagellum and assumed the condition of a swarm-spore. G, the swarm-spore become Amœboid. H, two Amœboid swarm-spores in close juxtaposition. I, the two Amœbœ fused together into a young plasmodium. J, the plasmodium more advanced; it has already begun to ramify and to take in nutriment: two nutriment-pellets are seen imbedded in its protoplasm. (After Greville and Cienkowski.)

sarcode offshoots are projected and again withdrawn in the manner of the pseudopodia of an  $Am \alpha ba$ , while the whole organism has been occasionally seen to abandon the support over which it had grown, and to creep over neighbouring surfaces, thus far resembling in all respects a colossal ramified  $Am \alpha ba$ .

From the surface of this sarcode-net there arise, as has just been said, the reproductive capsules or sporangia. In the soft plasma with which these are filled appear a multitude of nuclei, and the plasma then divides into a great number of roundish masses, in each of which a nucleus is enclosed. These are the young spores; they are accompanied in most species by a fibrous network, the "capillitium" (fig. 9, B, b), which fills up the intervals between the spores. When mature the sporangium bursts and allows the spores to escape (C). These are each enclosed in a thick membrane, which, after a time, becomes ruptured, and the little soft round mass of protoplasm which it had confined is set at liberty (D).

This little protoplasm lump encloses a nucleus with a minute central nucleolus, and contains one or two pulsating vacuoles (E); and soon after its escape it begins to show spontaneous movements, and to exhibit constant changes of form, while one end is drawn out into a long vibratile flagellum, by means of which, when placed in a drop of water under the microscope, it may be seen swimming about in the manner of the swarm-spore of an Alga (F). After a time it may be observed to withdraw its flagellum, emit and retract pseudopodia, and creep about like an  $Am\alpha ba$  over the stage of the microscope (G). It now takes in foreign bodies as nutriment, enveloping them in its substance ; it multiplies by selfdivision, and in all respects conducts itself like a genuine  $Am\alpha ba$ .

In the next place, a certain number of these amobiform bodies approach one another, come into close contact (H), and ultimately become completely fused together into a common mass of protoplasm (I). To the body thus formed by the fusion of the  $Am\infty b\alpha$ , Cienkowski has given the name of "plasmodium."

The plasmodium continues, like the simple amæbiform bodies of which it is composed, to grow by the ingestion of solid nutriment which it envelopes in its substance (J); it throws out ramifying and inosculating processes, and finally becomes converted into a protoplasmic network, which, in its turn, gives rise to sporangia with their contained spores, and thus completes the cycle of its development.

Under certain conditions not yet perfectly understood the

Myxomyceta have been observed to pass from an active motile state into a resting state; and this may occur in both swarmspores and plasmodium. In the case of the swarm-spores, these bodies, when passing into the resting state, assume a spherical form, and become surrounded by a delicate membrane or by a firm external layer of thin protoplasm. In this condition, in which they constitute the "microcysts" of Cienkowski, they may remain, after complete desiccation, in a dormant state for more than two months; and on being again placed in water they soon resume their original activity.

But the plasmodium itself, as well as the swarm-spore, may pass into a resting state. After withdrawing its finer branches, and expelling such solid ingesta as may be included in it, its motions gradually cease, it breaks up into a multitude of polyhedral cells, and the whole body dries into a horny brittle mass, to which the term "sclerotium" has been given.

It sometimes happens that the plasmodium, instead of forming a continuous sclerotium, breaks up into separate pieces of very unequal size, which withdraw their projecting branches and assume the form of smooth spheres, round which a thick membrane is excreted. Within this outer membrane the protoplasm contracts and forms on its surface a second membrane. To these cell-like bodies Cienkowski has given the name of "thick-walled cysts."

Both these resting states of the plasmodium may, like that of the swarm-spores, undergo complete desiccation, and thus continue for many months in an inactive state without losing their vitality. When the dry sclerotium is placed in water, it immediately swells up, and after a time its cells again flow together into an anœboid protoplasm. So also when the thick-walled cysts, after remaining long desiccated, are similarly treated, their membrane will become ruptured, and the contained protoplasm will escape and begin to throw out pseudopodia and glide about like an Amœba, and engulf within its substance foreign bodies for nutriment, while several may unite by fusion into larger amœbiform masses and thus give rise in their turn to new plasmodia.

In a subsequent paper\* Cienkowski describes the plasmodium of an unknown Myxomycetewhich occurs in fresh water in the form of a sarcode network, and which has enabled him to add some interesting facts to our knowledge of the plasmodium.

\* Cienkowski, "Ueber einige Rhizopoden und verwandte Organismen," Archiv f. mikr. Anat. 1875. He found that a fragment broken off from this plasmodial network moves about independently, and he saw it throw out a long pointed pseudopodium which attached itself to an Alga, penetrated its walls and sucked out its contents in the manner of a *Vampyrella*, another simple sarcode organism to which we shall presently refer.

Whether the Myxomyceta should take their place in the animal or vegetable kingdom is a question which in the present state of our knowledge it is impossible to answer. Haeckel has evaded the difficulty by placing them, along with a number of other doubtful organisms, in his kingdom of the *Protista*, which he regards as holding an intermediate place between animals and plants.

Cienkowski has followed his researches on the Myxomyceta by another important memoir on a group of minute sarcode organisms to which he has assigned the name of  $Monadina^*$ . During certain phases of their development they resemble in many respects the well-known zoospores of the Algæ, and might, indeed, be so regarded, were it not that, like the swarm-spores of the Myxomyceta, they have been proved to pass through a special and peculiar cycle of development which entitles them to be viewed as an independent group.

Cienkowski has given us the life-history of five forms which he refers to his *Monadinæ*. Two or three of them may be here adduced with the view of giving an adequate conception of these remarkable organisms.

In the cells of decaying *Nitella* there may be found certain minute spindle-shaped very contractile bodies, which move about by the aid of cilia, and which closely resemble the swarm-spores of the *Myxomycetæ* or of the Algæ. Cienkowski has assigned to them the name of *Monas amyli*. After a time they lose their cilia, emit pseudopodia, and, assuming the form of an *Amæba*, creep about and take in foreign matter as nutriment by enveloping it in their soft protoplasm. Further, two or more of these amæbiform bodies may unite and become fused together into a plasmodium like that of the *Myxomycetæ*.

After enjoying for a time its free locomotive condition, Monas amyli passes into a resting state. The amœbiform body begins to harden itself on its surface into a continuous membrane, and thus becomes enclosed in a capsular covering. After continuing thus

\* Cienkowski, "Beiträge zur Kenntniss der Monaden," Arch. f. mikros. Anat. 1865.

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encysted for a certain time, the contents of the capsule become broken up into numerous separate masses of protoplasm, which finally escape in the form of the spindle-shaped zoospores found in the *Nitella*.



Protomonas Huxleyi.

A, fragment of a cylindrical diatom (*Rhizosolenia*) to which the *Protomonas*, B, in its encysted state, is attached. C, the cyst with its contents broken up into spherical non-nucleated protoplasm masses. E, the spherical masses, after having developed a flagellum, have become free swarm-spores by the rupture of the cyst. D, ameeboid condition assumed by the swarm-spore. F, the amœboid swarmspore having assumed the form of an *Actinophrys* by the emission of numerous fine pseudopodia. (After Haeckel.)

The generic name of *Monas*, under which Cienkowski has described this singular organism, has been changed by Haeckel\* into that of *Protomonas*, on the very tenable ground that the name of *Monas* had been long applied to a group of microscopic organisms which we should not be justified in confounding with the monads of Cienkowski. Haeckel has, moreover, described another representative of the genus, which he found in the Canary Islands attached to the surface of a floating diatom, and which he names *Protomonas Huxleyi*. He gives a very complete account of its life-history, which is in all essential points like that of *P. amyli*. \* Monographie der Moneren. I have taken Haeckel's figures (fig. 10) as affording an excellent illustration of the life-history of this remarkable group of organisms\*.

A still more remarkable genus of *Monadinæ* is *Vampyrella*, Cienkowski. Perhaps the most interesting of the three species of *Vampyrella* described by Cienkowski is the *V. spirogyræ* (fig. 11). This has long been known to algologists in the form of spherical brick-red capsules (B), which are often found attached to the filaments of the confervoid alga *Spirogyra*. It is, however, the merit of Cienkowski to have discovered the real nature of these capsules and to have satisfactorily traced their life-history.

The walls of the capsule are composed of two membranes. The inner gives the characteristic cellulose reaction, becoming blue when treated with sulphuric acid and iodine. The outer membrane, which in the older capsules is often absent, forms a soft nitrogenous layer. The contents of the capsule consist of a brick-red protoplasm with, usually, large dark irregular granules towards the centre caused by foreign matter which had been taken in as nutriment. By carefully continued observations the contents may be seen to divide into two or four portions (tetraspores) (C), and then to escape in the form of red  $Am\alpha ba$ -like bodies through round openings in different parts of the capsule. The dark bodies which remain behind in the capsule are the undigested remains of the nutriment.

The bodies which have thus become liberated appear to be destitute of nucleus and contractile vesicle. When released they assume the form of spherical masses of a red-coloured protoplasm (D), from the surface of which are emitted pointed pseudopodial rays like those of an *Actinophrys*. They are, however, very contractile and undergo constant change of form, drawing themselves out into strings and fine filaments, which tear asunder and again unite and send off branches and form fan-like expansions; while these ramified creeping masses of protoplasm can again contract themselves into a sphere.

When the *Vampyrella* in this condition is watched in water containing some plants of *Spirogyra*, it may be seen wandering about slowly until it strikes against one of the filaments of the alga. After gliding for some time over the surface of the filament it attaches itself to it if the filament be healthy and loaded with

\* Haeckel, "Nachträge zur Monographie der Moneren," Jenaische Zeitschr. 1871.

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Fig. 11.

Vampyrella spirogyræ.

A, the Vampyrella in the act of sucking out the contents of a Spirogyra-cell. B, the Vampyrella in its encysted state: a, nitrogenous covering: b, interior contents. C, the contents of the Vampyrella-cyst have become divided into tetraspores, and one of these is seen escaping as an Amæba-like Vampyrella. D, the free amœboid Vampyrella. (After Cienkowski.)

chlorophyl. We next find that it has begun to perforate the walls of the filament; and no sooner has it thus gained access to the interior than the protoplasmic lining ("primordial utricle") detaches itself from the cell-wall of the *Spirogyra*, and along with its adherent chlorophyl granules passes slowly into the body of the *Vampyrella* (A). As soon as the *Vampyrella* has thus gained possession of the contents of one cell it passes to another, and there repeats the process. In this way cell after cell is plundered of its contents; and now the *Vampyrella*, gorged with food, seats itself on some part of the alga, rolls itself into a ball, and quietly digests its prey.

The chlorophyl granules which had thus made their way into the interior of the *Vampyrella* now become gradually distributed through its entire body, and it then passes into the resting state (B), withdrawing its pseudopodia and excreting a soft nitrogenous covering, under which is formed a weak cellulose membrane. During this time the contents assume a red colour, and the encysted *Vampyrella* finally appears in the form of the red capsule with which the description of its life-history was commenced.

The only other species of *Vampyrella* which it will be necessary to refer to is one more recently described by Haeckel\*, who discovered it on the coast of Norway, and has assigned to it the name of *Vampyrella gomphonematis* (fig. 12). It appears to live exclusively on a species of *Gomphonema*, whose cells it envelopes and then sucks out their contents.

On the branches of the *Gomphonema* (A) are occasionally found, in place of the proper terminal cells of silica, a great abundance of clear red spherical capsules (a). These are the cysts of the *Vampyrella*.

The free-creeping V. gomphonematis (B) always appears as an irregular lump of protoplasm without nucleus or contractile vesicle, while from its surface there are emitted a great number of extremely fine pseudopodia.

In this condition it creeps over the stems and branches of the *Gomphonema*, adapting itself to the form of its support; and as soon as it has reached one of the terminal siliceous cells of the diatom, it extends itself over the entire cell so as completely to envelope it in a thin layer of protoplasm.

The plundering of the *Gomphonema*-cell now begins, and while a number of fine pseudopodia radiate from the body of the *Vampyrella* into the surrounding water, another portion of its protoplasm forces its way between the siliceous plates of the cell into the interior, and here appropriates the contents.

The empty siliceous cell (A, g, h) of the *Gomphonema* is now broken off from its stem and, as foreign indigestible matter, is cast out of the body of the *Vampyrella*, which continues to sit in the place of the cell and there digests its food in quiet. In this way it passes from cell to cell of the *Gomphonema*; and when it has thus plundered many cells, and by abundant nutriment has attained its full size, it begins gradually to withdraw its pseudopodia to round itself into a smooth sphere of protoplasm, to encyst itself by the exudation of a capsule, and pass into a resting state (a).

The encysted Vampyrella continues now to sit on the summit of the stem in the place of its last victim, and after remaining for some time in this condition of repose, the contents of the capsule

\* "Nachträge zur Monographie der Moneren," Jenaische Zeitschr. 1871.



Vampyrella gomphonematis.

A, a colony of Gomphonema attacked by numerous Vampyrella: a, an encysted Vampyrella; b, b, the cyst with its contents broken up into four tetraspores; c, e, a tetraspore transformed into the Vampyrella, which is escaping from the cyst, and has already begun to creep along a neighbouring branch; d, d, tetraspores still included in the cyst; f, a Vampyrella in the act of devouring the contents of a Gomphonema-cell; g, h, empty cells of the Gomphonema being cast out of the body of the Vampyrella. B, an isolated Vampyrella moving about by means of its extended pseudopodia. (After Haeckel.)

become divided into four similar parts (b, b). These are the tetraspores, which Cienkowski had already shown to constitute part of the developmental cycle of *Vampyrella*. In one spot of the capsule a small opening now appears, and through this the tetraspores slowly press themselves out (e), immediately emit pseudopodia, and assume the form of the creeping *Actinophrys*-like proto-

Fig. 12.

plasm lump which, as we have already seen, constitutes the fully developed state of the active and voracious *Vampyrella*.

Cienkowski divides his group of the Monadina into two subordinate ones :---

I. MONADINA ZOOSPOREA.—Reproduction effected by the formation of numerous mobile spores.

- 1. Monas (Protomonas, Haeckel).
- 2. Pseudospora.
- 3. Colpodella.

II. MONADINA TETRAPLASTA.—Reproduction effected by the formation of two or four *Actinophrys*-like bodies.

- 4. Vampyrella.
- 5. Nuclearia\*.

Among the most important researches on the lowest forms of life which must be brought under this review are those of Messrs. Dallinger and Drysdale on a group of minute flagellate organisms obtained from putrifying infusions of fish, and described by these investigators under the general name of "Monads"<sup>†</sup>.

By the aid of very high powers  $(\frac{1}{50}$  of an inch object-glass), and by employing an ingeniously constructed "moist chamber," Messrs. Dallinger and Drysdale have followed up the life-history of these organisms, and have discovered, common to them all, certain phenomena which are full of significance in the history of development.

Among several forms whose development has been carefully traced by them, we may take, as a sufficiently illustrative example, one to which they refer under the name of "the calycine monad ‡" (fig. 13). It has a conical shape (A),  $\frac{1}{1000}$  to  $\frac{1}{300}$  of an inch in length; the broad end carries four flagella, which spring from a common root, while the opposite end tapers away to a point. A shallow longitudinal depression extends backwards along each side, giving to the broad end an hourglass-shaped outline. It contains a large nucleus and two rhythmically contracting vacuoles.

The first phenomenon observed in its life-history is a multipli-

\* *Nuclearia* has been described above, and reasons given why it ought not to be associated with the *Monadina* of Cienkowski (see p. 386).

+ Rev. W. H. Dallinger and J. Drysdale, M.D., "Researches on the Life-History of the Monads," Monthly Microsc. Journ. vols. x.-xiii. 1873-75.

<sup>‡</sup> In no instance do the authors give a systematic name to the organisms which form the subject of their investigations, and to which they always refer under vernacular designations. cation by transverse fission. When this is about to take place the posterior or non-flagellate end becomes blunt and rounded, and the monad assumes a semiamœboid condition, the sarcode becoming irregular in outline (B). The common root of the flagella now splits, so that the four flagella are separated into two pairs, which recede more and more from one another until finally we find them situated on two diametrically opposite points of the



Development of "Calycine Monad."

A, fully developed monad, with nucleus and contractile vacuoles and four flagella. B, the monad in the semiamœboid state which precedes fission. C, the monad in the act of spontaneous fission. D, one of the two segments resulting from fission, each of the two flagella becoming doubled by longitudinal splitting. E, the amœboid condition which precedes fusion. F, two amœboid monads in the act of becoming fused into one another. H, the two blended bodies enclosed in a sac which is pouring out a cloud of sporules. J, I, G, the sporules becoming developed into the parent form. (After Dallinger and Drysdale.)

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body (C). In the mean time the nucleus has become divided into two, and between its halves the fission of the body proceeds until completed, and the two segments are set free. Each of these (D) is as yet provided with only two flagella, which immediately begin to split from the free end to the base, and the complete form of the parent monad with its four flagella is thus acquired. The two flagella during this act of splitting are attached to some fixed object by their distal ends and then thrown into a state of rapid vibration.

Besides the multitude of free-swimming, semiamæboid individuals thus noticed in the act of self-division, some (E) may be seen in which the amæboid condition is much more decided on the posterior end of the body from which pseudopodia are being constantly protruded, while the anterior end with its four flagella continues with but little change. The nucleus has become much larger.

In this condition the monad swims more and more slowly until, in some cases, it ceases entirely to swim, and moves about solely by the aid of pseudopodia, exactly like an *Amæba*.

If it now meet another in a similar condition, the amœboid parts unite and instantly blend into one another (F). This blending together of the two bodies becomes more and more intimate; the two sets of flagella unite and become fused into the general sarcode, the contractile vacuoles flow together and become inactive, the two nuclei also flow together, and, finally, the blending has become complete; all trace of the original form is lost, and all that remains is a distended roundish sac (H) which, after the lapse of some hours, will be seen to pour out in all directions, without evident rupture, clouds of excessively minute points which can be clearly defined as oval refringent corpuscles only by means of a magnifying-power of 2500 diameters. These were followed by the aid of a  $\frac{1}{50}$  of an inch object-glass, and their development traced into the form of the original conical monad with its four flagella.

The life-history thus traced in the "calycine monad" corresponds in all essential points with what the authors observed in the other species which formed the subject of their investigations. Multiplication by fission took place in every species, while a fusion together of two individuals would seem to be in every case a necessary phenomenon in the developmental cycle of the monad. In one form only, instead of inactive sporules of immeasurable minuteness following as a product of this fusion, the blended mass broke up into a multitude of minute flagellate young resembling the original parents in all points but size.

Messrs. Dallinger and Drysdale have further made a series of well-conducted observations on the capacity possessed by these "monads" of resisting high temperatures, and have arrived at results of great importance in their bearing on the evidence adduced by the advocates of the doctrine of spontaneous generation. They have thus shown that while the adult form is destroyed by a temperature comparatively low, the minute inactive sporules which result from the fusion of two monads may survive and become developed into the complete organism after exposure to a temperature of from 121° C. (258° Fahr.) to 140°.88 C. (300° Fahr.). This, however, occurs only in the case of the inactive sporules; the young active brood into which, in one of the species, the blended mass of sarcode breaks up only feebly survived a temperature of 82°.22 C. (180° Fahr.).

The capacity of resisting heat possessed by the inactive sporules has been estimated by the authors as bearing to that of the developed monad an average ratio of 11:6.

Haeckel records some additional observations on the structure of the Radiolaria<sup>\*</sup>. He had already † made it probable that the protoplasm of these is formed by the union of many true cells. As undoubted cells of the Radiolaria he had indicated the remarkable "yellow cells" and the intracapsular cells and alveolar cells. Recent observations have convinced him that the spherical clear vesicles which form the most important and constant constituent of the central capsule are genuine cells. He finds in them a true nucleus, and he regards it as very probable that they are reproductive cells.

This suspicion has been since confirmed by the observations of Cienkowski, who has seen the contents of the central capsule in *Collosphæra* break up into monadiform masses, which developed on one end a pair of cilia and escaped in the form of zoospores ‡. The ultimate destiny, however, of these bodies remains unknown.

It is well known that in *Actinosphærium Eichornii* (which with *Actinophrys sol* and most of the so-called freshwater Radiolarians constitute the group of the Heliozoa) numerous nuclei exist in the

\* "Beiträge zur Plastidentheorie," Jen. Zeitschr. vol. v.

† Die Radiolarien, 1862.

‡ Cienkowski, "Ueber Schwärmebildung bei Radiolarien," Archiv f. mikr. Anat. vol. vii. 1871. endosarc. These are regarded by Haeckel as indicating a true multicellular structure, which he compares with the multicellular contents of the central capsule in the Radiolaria. He has further shown that in the young state of various families of Radiolaria, though the central capsule is absent, the central part of the protoplasm-body includes a number of cells. He hence concludes that the young Radiolaria whose central capsule is as yet absent are morphologically equivalent to *Actinosphæria*. It should be borne in mind, however, that even though we adopt Haeckel's view of the multicellularity of *Actinosphæria*, the cells of this rhizopod would be indicated solely by nuclei without any differentiated territories of the surrounding protoplasm.

Haeckel has made the very interesting discovery that the socalled "yellow cells" of the Radiolaria contain a substance which cannot be distinguished from the starch of plants\*. Acted on by iodine the granular contents of these cells acquire an intense blue colour. The quantity of starch which is thus contained in the "yellow cells" of the Radiolaria is very great. In some cases more than half of the entire body of the Radiolarian consists of starch.

Among the most interesting and important contributions to our knowledge of the lowest sarcode organisms is Haeckel's 'Monograph of the *Monera*'<sup>†</sup>. Haeckel had already, in his 'Generelle Morphologie,' grouped together under the name of *Monera* certain organisms of the lowest conceivable kind. They consist of an absolutely homogeneous and structureless mass of sarcode, destitute in their fully developed and free-moving state of external investing membrane and of internal nucleus and contractile vacuole, and multiplying themselves by a self-division of their substance. They are the simplest of all organisms; indeed it is impossible to conceive of a living being reduced to an expression more simple.

No character has yet been discovered in them which would justify us in assigning them to the animal kingdom rather than to the vegetable, or to the vegetable rather than to the animal : and Haeckel unites them with the Rhizopoda, Flagellata, Diatomaceæ, and some other organisms slightly higher than these, in order to form an assemblage of low sarcodic forms which he regards as neither plants nor animals, but as holding an intermediate posi-

<sup>\*</sup> Beiträge zur Plastidentheorie.

<sup>† &</sup>quot;Monogr. der Moneren," Jenais. Zeitschr. 1868.

tion between the two. To this assemblage he assigns the rank of a separate kingdom, to which he gives the name of PROTISTA.

Haeckel had founded his group of the Monera on an organism which he had observed in the Mediterranean off Nice, and which he named *Protogenes primordialis*. It consists of a homogeneous ball of protoplasm, from whose surface thousands of fine threadlike pseudopodia, which frequently branch and become confluent



Fig. 14.

Protomyxa aurantiaca.

A, the *Protomyxa* in its encysted or resting state. B, the protoplasmic contents of the cyst have become broken up into a multitude of spherical segments. C, the protoplasm-spheres escaping from the cyst as flagellate swarm-spores. D, the free swarm-spores actively swimming about by means of their flagelliform processes. E, the swarm-spores after the withdrawal of the flagellum creeping about by means of pseudopodia in the manner of an *Amæba*. F, the fully developed *Protomyxa*: in the interior are seen numerous vacuoles (a) and an ingested diatom and infusorium (b, c); from the central protoplasm radiate a multitude of dendritically branched and anastomosing pseudopodia. (After Haeckel.) with one another, radiate in all directions. Nutriment is ingested in the same manner as by the true Rhizopoda, and reproduction is effected by a simple spontaneous division of the body into two halves without this phenomenon being preceded, as in other cases, by a motionless or encysted state.

In the present memoir Haeckel describes several genera of Monera. The Protomyza, of which we know only one species, P. aurantiaca (fig. 14), was found on an empty Spirula-shell in the Canary Islands. In its developed state (F) it forms minute stellar and arborescent figures of an orange-red colour, which spread over the surface of the shell and vividly remind us of the ramified contractile pigment-cells common in the skin of Amphibia and Fishes. Each star-like body presents a central mass of sarcode from which radiate numerous branches, which subdivide and inosculate and form a beautiful moving and changeable net of protoplasm not unlike that of the Myxomycetæ. Orange-red granules, to which the colour of the plasma is due, streamed in all directions through the sarcode-net. Foreign bodies also, such as pelagic Infusoria and Diatomaceæ, were seized by the protoplasm and engulfed as food in its substance, where they might be seen, along with the red granules, to be carried away in its currents.

No nucleus or definite contractile vesicle was present, though numerous floating and inconstant vacuoles were dispersed through its substance.

After a time an important change begins to take place. The currents become slower, the ramified processes become gradually withdrawn; and after the siliceous and other indigestible remains of the food are ejected, the whole body becomes rounded into a spherical mass. Round this a transparent cyst now becomes excreted, and the *Protomyxa* passes into a state of complete quiescence (A). These motionless encysted balls of orange-red protoplasm were also observed by Haeckel attached to the surface of the *Spirula*-shell, and their subsequent history was followed by him.

He found that after a time the contents of the cyst became slightly retracted from the walls, and then became broken up into a multitude of small, round, structureless, naked balls (B). After remaining in this condition unchanged for several days, the contained balls began to move within the cyst; and as the motion became more lively, the balls assumed a pyriform shape, in which one end was drawn out into a fine point. Soon after this the cyst burst (C), and a multitude of the red pear-shaped bodies issued from it and moved about in the surrounding water. It was soon seen that one end had become attenuated into a very fine tail or flagellum (D), so that the free sporules resembled the Flagellatæ, or the zoospores of an Alga. They were without a trace of nucleus, or of contractile vesicle, or of investing membrane, and consisted solely of minute naked masses of homogeneous protoplasm.

This swarming-period lasted about one day, and then the sporules lay quiet on the bottom of the vessel. The tail was drawn in, and the pear-shaped form was changed into that of an irregular roundish disk, from whose circumference pseudopodial processes began to be emitted. The sporule had now passed into the condition of an Amxba (E), and began, like an Amxba, to take in nutriment by engulfing it in its substance; and then vacuoles of inconstant size and position made their appearance within it.

Two or more of these Amæbæ were seen to unite and form a plasmodium. The pseudopodia became more and more branched and reticulated, and the condition of the orange-red dendritic patches, which crept over the Spirula-shell, and with which our history commenced, was finally attained.

It is thus seen that *Protomyxa* passes in the course of its development through an encysted or sedentary stage, and a free or mobile stage. The latter shows itself in three different successive forms:—1, that of a free-swimming flagellate; 2, that of a creeping  $Am\alpha ba$ ; and 3, that of a contractile protoplasm-net.

The genus *Myxastrum*, represented by *M. radians* (fig. 15), was also found by Haeckel in the Canary Islands. It consists of a small globular mass of homogeneous protoplasm (G), from whose whole periphery radiate a multitude of fine pseudopodia. It thus bears a close resemblance to the well-known *Actinophrys sol*, from which, however, it is separated by the absence of vacuolæ and by its remarkable mode of reproduction.

When the time for its reproduction approaches, Myxastrumradians retracts its pseudopodia, assumes the form of a smooth ball, encysts itself in the manner of *Protomyxa*, and becomes motionless (A). After a time the plasma mass within the cyst becomes divided by radiating furrows into numerous segments, which gradually assume a spindle-shape and become clothed with a thin siliceous membrane (B, C). These spindle-shaped bodies resemble *Naviculæ*, and if isolated might easily be taken for small Diatoms.

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They want, however, the nucleus of the Diatomaceæ. They are simple non-nucleated masses of protoplasm invested by their siliceous membrane.



Myxastrum radians.

A, the *Myxastrum* in its encysted resting state. B, the homogeneous contents of the cyst have become broken up by radial cleavage into numerous conical masses whose points touch one another in the centre of the sphere, and whose rounded bases are visible at the periphery. C, the conical segments of B have become fusiform, and each has excreted for itself a siliceous shell. The focus of the microscope is here directed upon a meridional plane so as to show the radial disposition of the fusiform spores. D, the free fusiform spore with its siliceous shell. E, the protoplasmic contents of the spore escaping from its siliceous shell. F, the homogeneous protoplasm of the spore which has entirely freed itself from its siliceous shell, and assumed a spherical form. G, the same protoplasm mass become the fully developed *Myxastrum*, with a multitude of fine pseudopodia radiating in all directions from its periphery. (After Haeckel.)

In this condition they remain for some time within the cyst, and then, by the rupture of this, escape and become dispersed in the surrounding water (D). Soon after this the homogeneous protoplasm issues through an aperture in one end of its siliceous covering (E), contracts itself into a ball (F), begins to emit radiating processes from its surface and to take in nourishment from without, and then by a process of simple growth acquires the condition of the adult *Myxastrum*.

Under the name of *Myxodictyum sociale*, Haeckel describes another representative of the Monera, which he obtained from the surface of the sea in the Bay of Algesiras. When taken it consisted of a group of roundish masses of homogeneous protoplasm, resembling small Actinophryses, from each of which radiated numerous fine branching and anastomosing filaments, which became confluent with those of the neighbouring masses, uniting the whole into a simple large plasma-net.

The uniting filaments resembled in all respects the pseudopodia of the true Rhizopoda, and the characteristic sarcode-currents might be seen in them passing from mass to mass. *Myxodictyum* would thus appear to represent a colony of Moners rather than a single individual; and Haeckel compares it in this respect with the polycytarian or social Radiolaria.

Nothing decided has been discovered regarding the reproduction of *Myxodictyum*, but it is probable that some of the masses detach themselves from the margin of the old colony and form new ones.

Those independent Amæba-like organisms which have neither nucleus nor contractile vesicle, and whose body consists  $c^{2}$  a perfectly structureless mass of protoplasm, have been, under the name of *Protamæba*, separated by Haeckel from the true Amæbæ, which always possess a nucleus and generally a vacuole, or even a true contractile vesicle.

Haeckel here describes his *Protamæba primitiva* (fig. 16), which he found among decaying leaves in the fine mud of a pond near Jena. It consists of a mass of absolutely homogeneous protoplasm, which emits from its periphery short blunt pseudopodia, and shows no differentiation of a more firm outer and a softer inner portion, as is seen in some other species of *Protamæba* and in most, probably all, of the true *Amœbæ*. It takes in nutriment by enveloping solid matter in its substance in the manner of the true *Amœbæ* and the *Amœba*-like blood-cells of animals : and it multiplies by the simplest form of non-sexual reproduction—the spontaneous division of its body without previously passing into a resting state.

Bodies entirely similar to these Protamæbæ occur as transi-

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tional stages in the development of some other Monera (*Protomyxæ*) as well as in that of the Gregarinæ. But the *Protamæbæ* of Haeckel are independent organisms directly reproducing themselves by spontaneous fission. The forms constituting the genus *Protamæba* are thus distinguished from the other Monera by their simple pseudopodia, which never anastomose with one another so as to form net-like expansions, and also by the fact that their reproduction is by simple self-division without this being preceded by an encysted or resting state. A similar form of reproduction exists in *Protogenes*, another genus of Monera; but here the pseudopodia are long thin branching processes which anastomose with one another and form protoplasm-nets.



Protamaba primitiva.

A, the *Protamaba* with short lobe-like pseudopodia. B, the same, with a longer pseudopodium. C, the same, in the act of self-division into two segments (a, b). (After Haeckel.)

Besides *Protamæba primitiva*, several other species of *Protamæba* have been since described by Haeckel\*.

A peculiar slimy substance dredged from depths of from 5000 to 25,000 feet in the Atlantic Ocean, during the exploring expedition of the 'Porcupine,' had been examined by Huxley, who concluded that it consists of living protoplasm, vast masses of which extend over wide areas of the sea-bottom. He assigned to this remarkable substance the name of *Bathybius*.

Associated with it and imbedded irregularly in the slime are certain calcareous concretions of a very definite shape. These have been named Coccoliths by Huxley. They are in the form either of simple disks (Discoliths), or of two such disks united to one another so as to form a body (Cyatholith) whose shape has been very aptly compared by Huxley to a shirt-stud. Besides

\* "Nachträge zur Monographie der Moneren," Jen. Zeit. 1871. LINN. JOUEN.-ZOOLOGY, VOL. XIII. 36 these, but occurring much more sparingly, have also been found small globular concretions resembling little heaps of Coccoliths. These have been named by Wallich, who first drew attention to them, Coccospheres. Both Coccoliths and Coccospheres are believed by Huxley to be proper parts of the *Bathybius* and formed by excretion from the protoplasm.

The *Bathybius* has been since subjected to a very exhaustive examination by Haeckel\*, who believes that he is able to confirm in all points the conclusions of Huxley, and arrives at the conviction that the bottom of the open ocean at depths below 5000 feet is covered with an enormous mass of free living protoplasm, which lingers there in the simplest and most primitive condition, having as yet acquired no definite form. He refers it to his group of Monera, and suggests that it may have originated by spontaneous generation (*Urzeugung*), a question, however, which he leaves for future investigations to decide.

The determination of *Bathybius* as an independent organism has not been confirmed by observations since made during the expedition of the 'Challenger.' What has been regarded as the same slimy material which had been examined by Huxley and Haeckel, in specimens preserved in alcohol, has been again examined on the spot, and the 'Challenger' explorers have declared their conviction that it is only an inorganic precipitate due to the action of the alcohol. With the views of able observers thus differing from one another, it will be wise to reserve judgment.

The origin of the Coccoliths and Coccospheres still remains undetermined. Haeckel has described under the name of *Myxobrachia*<sup>+</sup> a remarkable genus of Radiolaria characterized by the possession of one or several thick fleshy arms, which terminate each in a capitulum. These terminal capitula enclose numerous calcareous concretions exactly resembling the single-disk coccoliths and the coccospheres of *Bathybius*. Notwithstanding, however, the impossibility of distinguishing the concretions of the one from those of the other, Haeckel cannot consider *Myxobrachia* as the proper source of the multitudes of coccoliths which cover the bottom of the sea.

\* "Beiträge zur Plastidentheorie," Jena. Zeitschr. vol. v. †  $\mathit{Ibid.}$ 

In a subsequent memoir\*, Haeckel gives the following systematic arrangement of all hitherto known Monera :---

I.		Genera.	
GYMNOMONERA.	1.	Protamœba	5 species.
Monera without rest-	2.	Protogenes	1 species.
ing state or encys-	3.	Bathybius	1 species.
tation.	4.	Myxodictyum	1 species.
II.		Genera.	
II. Lepomonera.	(5.	Genera. Protomonas	2 species.
II. LEPOMONERA. Monera with resting	5. 6.	Genera. Protomonas Protomyxa	2 species. 1 species.
II. LEPOMONERA. Monera with resting state and encysta-	5. 6. 7.	Genera. Protomonas Protomyxa Vampyrella	2 species. 1 species. 4 species.

Of all these sixteen species, seven live in fresh water, the remaining nine in the sea.

One of the most extraordinary of all those very low organisms whose recent study has been rewarded by the discovery of new and significant facts is one to which Haeckel<sup>+</sup> has given the name of *Magosphæra* (fig. 17).

Attached to the filaments of a species of the confervoid genus *Cladophora* were noticed small spherical cells (A) of a pale yellow colour, surrounded by a thick membrane, and showing in the middle of their transparent protoplasm a large spherical nucleus with a nucleolus. The structure of these bodies was thus undistinguishable from that of a true animal egg, with its vitelline membrane, vitellus, germinal vesicle, and germinal spot.

This egg-like form constitutes the first stage of *Magosphæra*. In attaining the second (B), a phenomenon in all respects like that of the total cleavage of the yelk sets in. The nucleus of the cell breaks up by self-division into two nuclei, and the protoplasm of the cell has now become divided into two segments, each enveloping one of the nuclei. Thus are formed the first two cleavagespheres, each of which in its turn, dividing into two, exactly repeats the phenomenon (C). And the process is continued (D) precisely as in ordinary yelk-cleavage, until with the fifth segmentation thirty-two cleavage-spheres or daughter cells are produced, and the process of segmentation is completed.

\* "Nachträge zur Monographie der Moneren," Jena. Zeitschr. 1871.

† Haeckel, "Die Catallacten, eine neue Protisten-Gruppe," Jena. Zeitschr. Band vi. 1871. The thirty-two daughter cells into which the egg-like cell has thus broken up now begin to show amœboid movements within their common investing membrane. At the same time they emit



Fig. 17.

### Magosphæra planula.

A, unicellular encysted condition. B, the cyst containing two cells; the single cell divided into two by the first act of segmentation. C, the contents of the cyst divided into four cells by continued segmentation. D, the contents of the cyst divided into sixteen cells by still further segmentation. E, the multicellular sphere resulting from repeated segmentation has forsaken the cyst, and now swims about by means of vibratile cilia. (Viewed from the surface.) F, the ciliated sphere viewed in optical section through its centre, so that ten of its component cells are seen in a meridional plane. G, an isolated ciliated cell with long tail. H, the cell having lost its cilia and assumed an amceboid form. (After Haeckel.)

from their surface small, blunt, irregular, pseudopodial projections. These gradually become more pointed, thinner, and longer; their motions become more lively, and the amœboid pseudopodia pass into vibratile cilia.

The change of pseudopodia into vibratile cilia had been already shown by Haeckel\* to occur in other instances, and has been regarded by him as proving the identity of amœboid protoplasmmotion with ciliary motion. I am enabled to bring forward a confirmation of this view in the apparent passing of pseudopodia into cilia on the gastric surface of Myriothela<sup>†</sup>.

The spherical cell-heap whose surface has in this way clothed itself with vibratile cilia begins by the aid of these to rotate slowly within the egg-membrane. This is at last ruptured, and the ciliated sphere escapes and swims about by means of its cilia in the surrounding water (E).

The Magosphæra is now in the condition of a multicellular ciliated sphere so closely resembling one of Ehrenberg's Volvocineæ, that if its history were not known it would, without hesitation, be placed in this group as a genus closely allied to if not identical with the Synura of Ehrenberg.

The cells, which have a spherical form, or are more or less polyhedral from mutual pressure, now become regularly pyriform, and are seen to be united in the centre of the sphere by their elongated ends (F), while the peripheral end is rounded off and furnished with cilia, which appear to sit upon the margin of this end in a circle interrupted at one side by a spiral arrangement, as in the peristome of *Vorticella*, &c.

The cells have no membrane, and the intervals between them are filled with a watery, structureless, jelly-like secretion from their surface, as in the *Volvocineæ*. Every cell encloses in its protoplasm a nucleolated nucleus surrounded by granules, and possesses also a contractile vesicle.

After the *Magosphæra* has thus continued for some time swimming about in the sea as a ciliated sphere, it begins to resolve itself into its constituent elements. The single ciliated cells now separate from one another and swim about independently (G). In this state they might be easily taken for peritrichal ciliate Infusoria, or for isolated cilia-cells of the epithelium of the higher animals. These separate cells are very contractile, and are con-

<sup>\*</sup> Beiträge zur Plastidentheorie.

<sup>+ &</sup>quot;On the Structure and Development of Myriothela," Phil. Trans. 1875.

stantly changing their shape from fusiform to spherical. They take in coloured food through the cilia-disk, though no constant mouth could be detected.

From the stage represented by the isolated cilia-cell, Magosphæra next passes into the condition of a genuine Amacba (H). In this stage it appears as a simple naked nucleated cell, like all genuine Amacba. The pseudopodia are thin, conical, and pointed, like those of Auerbach's Amacba actinophora or his A. bilimbosa. The nucleus and contractile vesicle are still present, as in the isolated cilia-cell, and we can distinguish, as in most of the true Amacbaa, an external firmer layer and an internal softer one. Solid food is taken in as in the isolated cilia-cell. The ingestion, however, is not, as in the latter, confined to a definite spot, but may take place indifferently from any part of the surface.

The Amcba-stage would seem to close the cycle of development; and though Haeckel has not succeeded in actually following up its life-history, it seems pretty certain that after the Amcba has increased in size by the reception of nutriment, it once more encysts itself and returns to the egg-stage with which our examination began.

In this most remarkable life-history, *Magosphæra* has passed successively through the following stages :---

1. A unicellular resting stage, indistinguishable morphologically from a genuine egg (A).

By a process of cleavage which in all respects resembles a true vitellary segmentation this passes into

2. The condition of a multicellular ciliated sphere, in which it resembles a form of the *Volvocine* $\alpha$  (E).

3. A simple isolated cilia-cell, representing the condition of a peritrichal ciliate Infusorium (F).

4. An amœboid cell indistinguishable from a genuine Amœba (H).

The characters thus presented by *Magosphæra* appear to Haeckel to justify him in regarding it as a member of his group of the Protista; and from the fact of its representing in the cycle of its development so many different independent forms, he makes it the type of a distinct section of this group, to which he assigns the name of CATALLACTA.

Magosphæra, however, would seem to be related to the Infusoria at least as nearly as to the Rhizopoda. It is plainly a transitionform by which the one group passes into the other. I have thus attempted, in the present Address and in that of last year, to bring before you in rapid review a large number of organisms with whose true structure and life-history biologists have only quite recently become acquainted. They are among the most interesting of those simple beings which, standing on the confines of organization, constitute the group of the Rhizopoda in the wider signification of this word. The marine forms represented by the Radiolaria and Foraminifera have been only incidentally touched on; but the freshwater forms, with such dwellers in the sea as most directly represent them, have been here examined in all their most important features.

Notwithstanding, however, the excellent work which we owe to numerous continental observers, and in our own country to W. Archer, much still remains to be known of the structure and lifehistory of the freshwater Rhizopoda, and a rich field for exploration lies open to the microscopic observer—a field, too, of easy access; for, unlike the objects which form the study of the marine zoologist, these Rhizopods of fresh water may be found in almost every inland locality wherever there are undisturbed pools, or weedy ditches, or slowly running streams, in the shallow pools which collect upon the wild moors where there is nothing to intercept the heat and light of the summer sun, and even in gloomy ponds shaded from sunlight by overhanging trees and half-filled with decaying leaves.

While thus bringing before you the results of recent researches, my exposition has necessarily assumed the character of a general survey of the freshwater Rhizopoda and of the Monera and other nearly allied organisms; for almost all the knowledge we possess of these simple forms of life has been derived from investigations carried on within the last few years.

I have hopes, therefore, that the exposition which I have endeavoured to give you in last year's Anniversary Address and in that of the present year may be of some value in affording aid to the worker in one of the most interesting fields of microscopical research.